# On the Dispersal of Hair Lichens (*Bryoria*) in High-Elevation Oldgrowth Conifer Forests

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Arboreal hair lichens belonging to the genus *Bryoria* provide crucial winter food for the threatened Mountain ecotype of the Woodland Caribou. Earlier studies suggest that the reliance of many *Bryoria* species on thallus fragmentation as a primary mode of reproduction can lead to low dispersal rates. This paper examines the occurrence of thallus fragments over a snow-covered subalpine meadow following a late winter windstorm of moderate force. Fragment densities were greatest immediately downwind of the forest edge, but remained substantial even at a distance of 2 km. This suggests that dispersal is not limiting for at least some *Bryoria* species at subalpine elevations. It is proposed that the ecological requirement of *Bryoria fremontii* and *B. pseudofuscescens* for well-ventilated habitats considerably enhances their ability to inoculate young, regenerating stands over considerable distances. Their observed general absence in young trees is probably a function of substrate limitations rather than of limitations of dispersal.

Key Words: *Bryoria fremontii, Bryoria pseudofuscescens, Nodobryoria oregana*, arboreal lichens, conifer forests, wind dispersal, Wells Gray Provincial Park, British Columbia.

Mountain Caribou are a globally threatened ecotype of the Woodland Caribou *(Rangifer tarandus caribou)* (see Thomas and Gray 2001*). Restricted to southern inland British Columbia and adjacent Washington and Idaho (Paquet 1997), these animals spend much of each winter at upper forested elevations. Here snowpacks two to four metres deep make cratering for terrestrial forage impractical; to survive, wintering Caribou must depend on a nearly exclusive diet of arboreal hair lichens (Edwards and Ritcey 1960; Rominger et al. 1996).

Thirteen species of hair lichens are known from the upper-elevation Engelmann Spruce *(Picea engelmannii)* — Subalpine Fir *(Abies lasiocarpa)* forests (henceforth ESSF) of inland British Columbia (Goward and Ahti 1992; and later observations). Ten of these are members of the genus *Bryoria*, while two belong in *Nodobryoria*, and one in *Alectoria*. All are pendulous species with a hair-like morphology, and all colonize the branches of conifers.

In boreal and montane ecosystems, hair lichens are typically more abundant in oldgrowth forests than in younger forest types (Esseen et al. 1996; McCune 1993; Peterson and McCune 2001). The inability of hair lichens to accumulate to heavy loadings in young forests can potentially be attributed to one or more of four causes: (1) unsuitable bark chemistry associated with young branches; (2) slow growth rates; (3) unsuitable microclimatic conditions; and (4) inefficient mechanisms of dispersal. The respective roles of these mechanisms in the distributional ecology of hair lichens in high-elevation oldgrowth forests are briefly discussed below.

## Branch Chemistry

Young tree branches occur in young and old stands alike. If the chemistry of young branches were truly limiting to hair lichen establishment, then hair lichens should invariably be lacking from this substrate. Yet young branches in old stands can actually support rather high loadings of hair lichen, at least under well-ventilated conditions (Goward 1998). On this evidence, bark chemistry seems unlikely to be prohibitive to hair lichen development in the ESSF. Recent research, however, suggests that an elevated bark pH may adversely affect hair lichen establishment in some lower elevation forests (Goward and Arsenault 2003).

## Growth Rates

Lichens are often assumed to be slow-growing organisms. Recent studies by Stevenson (1979), Esseen et al. (1996), and McCune et al. (1996), however, indicate that hair lichens grow more rapidly than previously thought, with annual increments in the order of 5% to 30%. This is consistent with the observation that at least some *Bryoria* species attain mature proportions in under 20 years (Goward, unpublished). Slow growth rates per se are thus unlikely to be responsible for the low hair lichen loadings characteristic of young forests.

## Microclimate

Goward (1998) has suggested that hair lichen biomass is controlled primarily by a pronounced sensitivity to prolonged wetting. Viewed from this perspective, within-canopy shifts in hair lichen loadings can be expected to correspond to age-related changes
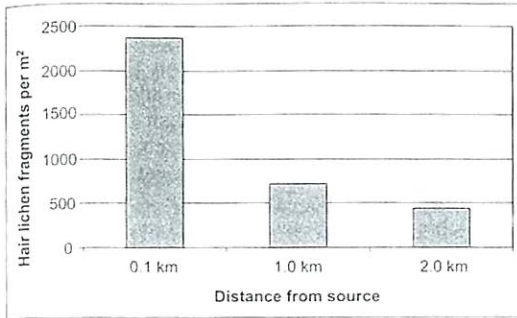
FIGURE 1. Wind-scattered hair lichen fragments in relation to distance from source, 7 April 1996, Fight Lake Meadow, Wells Gray Provincial Park, British Columbia.

in forest structure. As a forest ages, the creation of canopy gaps exposes hair lichens to gradually increasing levels of ventilation. At the same time, the centrifugal architecture of conifers ensures an increasing incidence of microniches sheltered from frequent wetting. Many hair lichens, especially in the genus *Bryoria*, appear to be specially adapted to these conditions (Campbell and Coxson 2001), suggesting that microclimate can play a significant role in the stand-level distribution of these species.

*Dispersal*

Few quantitative studies involving hair lichen dispersal have been undertaken to date. In a field trial in 10-15-year-old Douglas-fir *(Pseudotsuga menziesii)* plantations on Vancouver Island, Stevenson (1988) found that hair lichen colonization on second-year twigs declines rapidly with increasing distance from mature timber. Colonization rates decreased to about 50% of maximum at 100 m from the forest edge, then to 10-15% at 300-400 m, and finally to less than 5% beyond 450 m. Based on these findings, Stevenson concluded that dispersal limitations can delay lichen development in young forests. Dettki (1998) and Dettki et al. (2000), working in older forests in Sweden, arrived at a similar conclusion.

The above studies notwithstanding, it can be argued that rates of hair lichen dispersal into young stands are unlikely to affect lichen biomass in the same stands many decades later. As young, regenerating forests develop, tree branches initially exposed to open conditions are increasingly sheltered from ventilation (Oliver and Larson 1996). The corresponding increase in ambient humidity entrains a gradual decline in hair lichen abundance (Goward 1998). Only much later, as stand thinning gives rise to a more open canopy structure, do hair lichens once again prosper in the lower canopy. By that time, however, the upper forest canopy acts as a prominent source of hair lichen diaspores (Goward, in preparation).

The oldgrowth ESSF forests of British Columbia are currently undergoing severe fragmentation due to industrial-scale forestry. Earlier studies on hair lichen reproduction suggest that dispersal limititations in *Alectoria and Bryoria* could impose significant constraints on their ability to colonize the resulting plantation stands (see Dettki et al. 2000). Given the importance of hair lichens in the winter ecology of Mountain Caribou, it would be useful to determine to what extent dispersal is likely to be limiting under these conditions. The primary objective of this study is to report on recent findings pertaining to this question. Special emphasis will be placed on those hair lichen species assumed to provide significant winter forage for Caribou.

*Hair Lichens as Forage for Wintering Caribou in ESSF Forests*

Little information is available concerning the differential use of hair lichen species by foraging caribou. That some species, however, are less important than others is well documented. Tracking studies by Rominger et al. (1996, 2000) have shown that *Alectoria sarmentosa* is generally not consumed by caribou, except in late autumn, when other food sources are scarce. Possibly this can be accounted for by the relatively low crude protein levels characteristic of this species (Antifeau 1987; Rominger et al. 1996).

Several other hair lichens can probably also be discounted as key forage species for caribou. *Bryoria capillaris, B. implexa, B. lanestris,* and *B. simplicior,* for example, are all rather sparse in the ESSF (Goward and Ahti 1992) and are therefore unlikely to be consumed in quantity. Also infrequent is *Bryoria tortuosa* which, in addition, may be unpalatable owing to high concentrations of vulpinic acid (Brodo and Hawksworth 1977). *Bryoria chalybeiformis* and *Nodobryoria abbreviata,* while slightly more common, are small species restricted in the ESSF to the upper canopy.

Five hair lichen species are much more widely available. Two of these, *B. fuscescens* and *B. glabra,* are most common in rather poorly ventilated sites, usually in the lower canopy (Goward and Campbell, in preparation). These species bear copious tiny powdery outgrowths called soredia. When dislodged, soredia act as asexual reproductive propagules apparently highly efficient at dispersal (Bailey 1976).

Of the remaining species, *Bryoria pseudofuscescens* and *Nodobryoria oregana* lack soredia, whereas *B. fremontii* occasionally produces them, albeit rarely at upper forested elevations (Goward, unpublished observations). These species are most abundant in well-ventilated habitats, especially the

crowns of old trees, where *B. fremontii* and *B. pseud-ofuscescens* often accumulate to exceptionally heavy loadings. In the lower canopy, they are usually much less prolific, being subject to periodic die-backs (Goward 1998; Goward and Campbell, in preparation). Only in highly exposed sites does the lower canopy support these species in abundance; such sites are highly sought after by foraging caribou (Rominger et al. 1996).

## Study Area And Methods

The field portion of this study was conducted at 1850 m in the upper "parkland" forests of Wells Gray Provincial Park (52°N, 120°W). The area is known locally as "Fight Lake Meadow": a shallow, flat-bottomed basin roughly 1 km (east-west) by 2 km (north-south), and surrounded by forested slopes supporting *Abies lasiocarpa* and *Picea engelmannii*. Bioclimatically, Fight Lake Meadow belongs in the orohemiarctic subzone of Tuhkanen (1984) and in the Engelmann Spruce — Subalpine Fir Zone of Meidinger and Pojar (1991). For a more complete description, see Hämet-Ahti (1978) and Goward and Hickson (1995).

In 1996, a two-metre snowpack had accumulated on Fight Lake Meadow by early April. On the morning of 7 April, the surface of the snowpack was covered by a 5 cm layer of fresh snow. A strong southeast wind arose later in the day, accompanied by thawing temperatures. The wind persisted for approximately 18 hours, causing the snow to settle.

After the wind had abated, copious hair lichen fragments could be observed scattered over the surface of the snow. As these fragments appeared to be nonrandomly distributed, a plot study was conducted to examine their spatial distribution. Three 10 m × 10 m plots were established along a north-south transect running the length of the meadow. The first plot was located 100 m from the south end of the meadow, close to the presumed source of the hair lichen fragments. The second plot was established in the centre of the meadow, approximately 1 km north of the first plot. The third plot was situated near the northern end of the meadow, approximately 100 m from the forest edge. Within each of these plots, ten 1 m × 1 m quadrats were established. The position of each quadrat was pre-assigned using two series of randomly generated single-digit numbers. The first series determined the *y* axis on a cartesian grid, while the second series provided the *x* axis.

Within each quadrat, a careful enumeration was made of hair lichen fragments larger than about 3 mm. For convenience, dark fragments were recorded as "*Bryoria*", notwithstanding the additional presence of *Nodobryoria*. Pale greenish fragments of *Alectoria sarmentosa* were also searched for. Within each plot, an attempt was made to identify the largest hair lichen fragments. The presence of nonsorediate hair lichens — *B. fremontii*, *B. pseudofuscescens*, and *N. oregana* — was especially noted. Also recorded was the number of conifer seeds occurring in each plot.

## Results

The data are summarized in Table 1. The plot located closest to the presumed fragment source yielded 2371 *Bryoria* fragments. By contrast, the intermediate plot had 721 fragments, while the plot near the northern edge of the meadow had only 445 fragments. Thus the total number of *Bryoria* fragments observed during this study was 3537. Proportionately few of these appeared to be sorediate, though only the larger thalli could be assessed for soredia. Only one fragment of *Alectoria sarmentosa* was detected.

The largest *Bryoria* fragments noted in each of the plots were 38 cm, 8 cm, and 6 cm long in the southern, intermediate, and northern plots, respectively. Nonsorediate thalli identifiable as *B. "fremontii"* (presumably including *B. pseudofuscescens*) and *Nodobryoria oregana* were observed throughout.

Conifer seeds followed a similar trend, with 23 noted in the southern plot, four in the intermediate plot, and none in the northern plot.

## Discussion

Successful dispersal by lichen propagules is a four-step process, consisting of liberation, transport, deposition, and establishment (Bailey 1976). This study illustrates the power of a single windstorm to liberate and transport hair lichen fragments across a snow-covered meadow. The results suggest that fragment densities 100 m from the forest edge exceed two million fragments per hectare. Even at a distance of 2 km from the parent stand, densities are still very high, at roughly 400 000 lichen fragments per hectare. Presumably many of the latter fragments could have been carried to even greater distances, were it not for the 2 km limit imposed by the meadow itself. It should be noted that these comments

TABLE 1. Hair lichen fragments over fresh snow in a subalpine meadow at three distances from the forest edge.

| QUADRAT | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.1 km | 237 | 268 | 250 | 232 | 218 | 241 | 225 | 217 | 225 | 258 | 2371 |
| 1.0 km | 54 | 52 | 64 | 77 | 74 | 80 | 85 | 80 | 67 | 88 | 721 |
| 2.0 km | 35 | 53 | 38 | 35 | 46 | 47 | 53 | 39 | 49 | 50 | 445 |

apply predominantly to nonsorediate species of *Bryoria*; very few sorediate thalli were noted, though this could have been an artifact of the small size of the thallus fragments. *Alectoria sarmentosa* was virtually absent from the study plots, suggesting that fragmentation in this species plays a minor role in medium-range dispersal (see also Dettki et al. 2000).

The northern plot was situated only 100 m from the north edge of the meadow, thus raising the possibility that fragment densities on the snow surface could have been affected by proximity to the adjacent forest. Two scenarios can be advanced: first that reduced wind speeds associated with the forest edge led to enhanced fragment deposition; and second, that hair lichens growing in the adjacent forest constituted a secondary source of lichen fragments, i.e., owing to air turbulence at the forest edge. Neither of these scenarios seems likely to apply in the present instance: first because upwind air flow should be affected to a distance of only three tree lengths (i.e., 50-60 m) from the forest edge (Oke 1978), and second because outward air turbulence from the forest edge ought to have resulted in the transport of at least some conifer seeds into this plot. Compare, by contrast, the presence of four seeds in the intermediate plot, and 23 seeds in the southern plot.

It is of course unknown what proportion of the hair lichen fragments liberated over Fight Lake Meadow during a late winter windstorm in 1996 actually became entangled in the branches of conifers. Nor can it be determined what percentage of the entangled fragments later developed into new lichen thalli. The present observations, however, are consistent with the hypothesis that wind dispersal is of central importance to the life history of at least some hair lichen species in the ESSF (see also Esseen 1985). Indeed, in the absence of wind dispersal, it would be difficult to account for the heavy biomass of nonsorediate hair lichens (e.g., *B. fremontii*, *B. pseudofuscescens*, and *Nodobryoria oregana*) on solitary trees hundreds of metres from the forest edge. Casual observation suggests that hair lichen community structure on such trees is indistinguishable from that on similar trees much closer to the forest (Goward, unpublished data).

Any major wind event is presumably capable of liberating hair lichen thalli in great numbers. Windstorms occur throughout the year in the ESSF, suggesting that the periodic relocation of hair lichen fragments to the branches of trees is probably a year-round phenomenon. Recent studies, however, suggest that the highest wind speeds occur in winter (Campbell and Coxson 2001), when surface irregularities are covered by snow; this is likely to enhance the medium-distance transport of *Bryoria* thallus fragments.

In an earlier study in southern Wells Gray Park, Edwards et al. (1960) estimated that oldgrowth ESSF forests support as much as 3300 kg of hair lichen biomass per hectare. The fact that the heaviest loadings develop in highly ventilated sites, usually in the upper canopy (Goward, 2003), is probably causally related to the overwhelming abundance of this genus in oldgrowth forests. The close association of at least the nonsorediate *Bryoria* species with sites promoting optimum conditions for thallus liberation and transport doubtless results in dispersal efficiencies much greater than in lowland regions less exposed to wind. Lesser wind strength could thus partly account for the apparent discrepancies between this study, in which hair lichen fragments are wind-transported at least 2 km, and earlier studies reporting pronounced fragment declines beyond about 100 m from the source area (Stevenson 1988; Dettki 1988; Dettki et al. 2000). Other mechanisms of dispersal are probably of greater importance in the sorediate species *B. fuscescens* and *B. glabra*, which are most abundant in portions of the canopy less exposed to wind.

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